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Canada
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Prepared by
Forest Service
U.S. Dept. of Agriculture
Northeastern Forest
Experiment Station
Broomall, PA 19008

GTR-NE-99

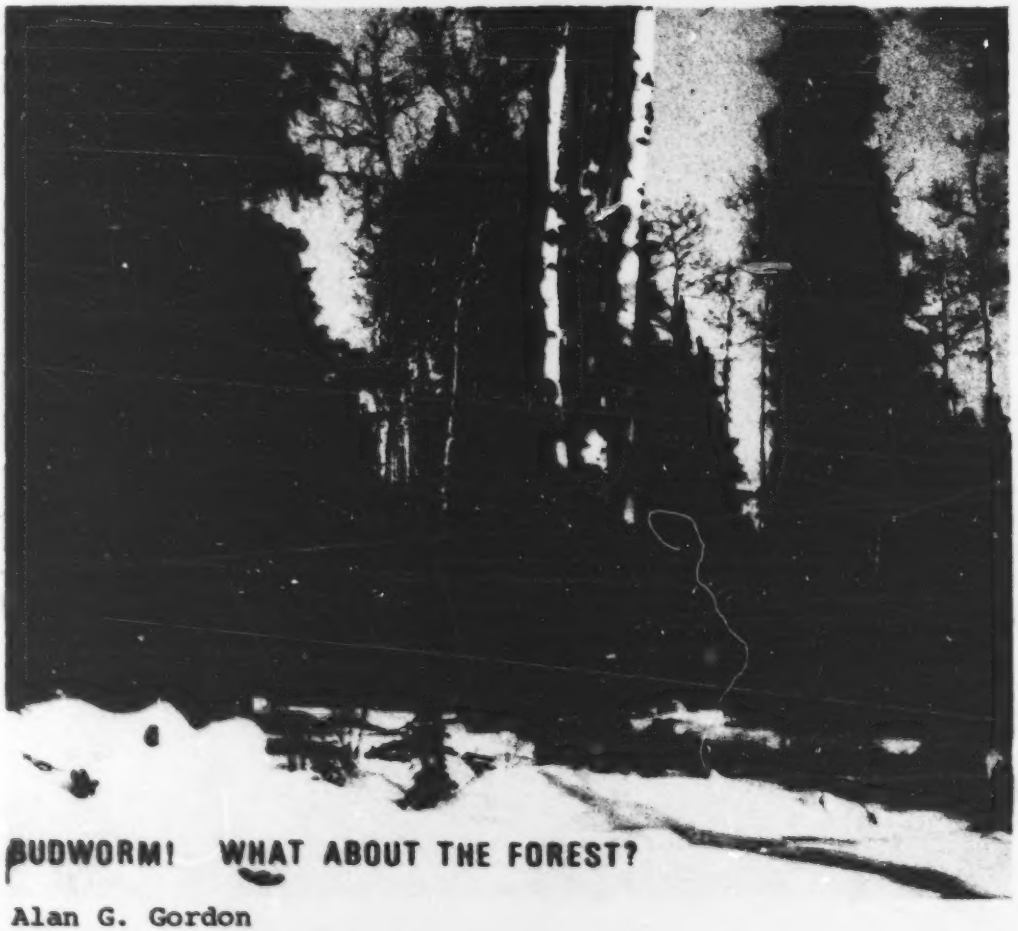
1985

Ministry of
Natural
Resources
Ontario

Spruce-Fir Management and Spruce Budworm

Society of American Foresters Region VI Technical Conference

SAF 84-07



BUDWORM! WHAT ABOUT THE FOREST?

Alan G. Gordon

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pp. 3-29

SPRUCE-FIR MANAGEMENT

AND

SPRUCE BUDWORM

Society of American Foresters

Region VI Technical Conference
April 24-26, 1984
Ramada Inn
Burlington, VT

Sponsors

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"BUDWORM! WHAT ABOUT THE FOREST?"

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The importance of the spruce and spruce-fir cover types in eastern North America is outlined.

Biogeographic history of spruce and fir is explained in relation to distribution during the Pleistocene. Evolution of the genus Picea is discussed with respect to continental drift. White spruce is essentially modern, dating from the Pliocene. Red spruce is an older species dating, with Arcto-Tertiary floral associates, from Tertiary times or perhaps earlier. Some genecological concepts are identified. The genetic distance as related to cross compatibility, particularly in white spruce, is outlined.

The consequences of long selected tolerances not only affected migration and present distribution but also affect management of modern stands. Respective nutrient uptake patterns, productivity and nutrient cycling strategies are demonstrated.

Finally, stand structures and dynamics of white spruce-fir and red spruce-fir forests are related to budworm activity.

Keywords: Spruce-fir; Picea glauca; P. rubens; P. mariana; Abies balsamea; Pleistocene; species assemblages; migration; ecological variation; productivity; nutrient cycling; evolution; paleobotany; genecology; crown form; hybridization; stand dynamics; budworm.

A year or so ago, I attended a Canada-Ontario Joint Forest Research Symposium in Timmins, Ontario entitled "The spruce budworm problem in Ontario - Real or Imaginary." When I came home, I discussed the meeting in general with my wife Jeanne and a number of the papers in particular. She listened with some comment for about half an hour and finally, in exasperation, breaking in, said, "Budworm! What about the forest?" That remark gave me the title of this presentation, an overview of the spruce and spruce-fir forest.

Extent and Importance of the Eastern Spruce-fir Forest

At the outset, I would like to provide an estimate of the enormous extent of the productive spruce and spruce-fir forest of Canada and the United States. Table 1 indicates the total area and volume for eight central and northeastern states. It may be seen that in this area there

Table 1. Area and volume of Stocked Productive Spruce and spruce-fir forest land*

State	Area 1000 ha	Volume 1000 m^3
MAINE	272	368,167
NEW HAMPSHIRE	25	52,620
VERMONT	16	37,581
CONNECTICUT	7	5,494
NEW YORK	319	54,461
MICHIGAN	83	67,800
WISCONSIN	93	36,080
MINNESOTA	647	45,623
Total	1,462	667,826

*data after USDA Forest Service (1982)

Table 2. Area and volume of stocked productive spruce and spruce-fir forest land*

Province	Area 1000 ha	Volume 1000 m^3
NEWFOUNDLAND	7,297	428,629
NOVA SCOTIA[1]	1,751	124,581
P.E.I.	165	22,036
NEW BRUNSWICK[2]	3,197	280,321
QUEBEC[3]	33,027	2,792,854
ONTARIO[4]	15,240	1,473,164
Total	60,677	5,121,585

*data after Bonner (1982)
Supplemental data courtesy:

[1]F. Wellings, Forest Resources, Nova Scotia Dept. of Lands and Forests

[2]W. Clowater, Forest Development Survey, N.B. Dept. of Natural Resources

[3]D. Demerse, Service de l'inventoire Forestier, Québec Min. de Terres et Foréts

[4]J. Osborn, Forest Resources, Ontario Ministry of Natural Resources

are 1,462,000 hectares which are equivalent to about 5,624 square miles. The total productive volume stands at 667,826,000 cubic metres. The productive area for six Canadian provinces from Ontario eastward is 60,667,000 hectares or 234,184 square miles (Table 2). The standing volume carried on this area is 5,121,585,000 cubic metres. Since in a number of Canadian provinces black spruce is not separated from white spruce in inventory data, these data also contain extensive areas of black spruce. Some states and provinces, e.g. Minnesota and Nova Scotia, have a great deal of

their spruce and fir associated with hardwoods and the volumes of spruce and fir per hectare appear somewhat lower since hardwood volume is excluded in summation. The sheer extent, its current production and its productive potential provide an idea of the incredible value of these forests. The budworm, with its propensity for periodic epidemic outbreaks, can cause tremendous losses and, as such, is a major component of management consideration of the spruce-fir forest. In addition to the foregoing, the northern spruce-fir boreal forest or taiga also extends northwestwards through northern Manitoba, all the way to Alaska.

To give you some idea of the extent and nature of the harvest in northern Ontario and Quebec, Figure 1 illustrates about a half mile (0.8 km) of stacked full-tree logs. (In full-tree logging, the stump and roots are left on the site. The tops are usually brought out to a primary landing where branches are removed). These log decks are, in effect, a whole spruce forest turned on its side! The height of the near end of the pile is higher than a bus and it may be seen that the small ends of the logs lie away from the road. Another stack is decked up on the other side. There is a second corridor down the far side of these decks and more logs decked beyond. This whole forest will be cut, brought in to this landing and then moved out to a mill. The landing will be filled up again continuously.

Figure 1. Tree length log decks in northern Ontario.

Pleistocene History and the Migration of the Spruce-fir Forest

Figure 2 provides a diagram of North America during full glaciation illustrating the maximum extent of the glacial sheets at about 18,000 years ago. The important thing to note from this is that if one considers the extent of the ice, it may be realized that, apart from a slight possibility in a small unglaciated corner in southeastern Alberta, there was no part of the boreal forest occurring at that time in Canada. The total boreal forest was located south of the glacial front and entirely in what is now the United States. A large refugium-corridor, connected with Beringia (the unglaciated parts of Alaska, eastern Siberia and the land bridge between them) existed in the central Yukon plain of central Alaska and extended partly into Canada, between the Laurentide and Cordilleran ice sheets. This refugium-corridor was, however, not as convenient as we may wish to presume for the survival of trees and forests.

The area was associated with large ice fronts and the climate was known to be somewhat dry and extremely cold. Flora from pollen diagram and mammalian remains from interior Alaska indicate that the area was essentially a dry steppe-like grassland in some areas, while seemingly a cold steppe tundra in others. While it is known that there were moderate amounts of both white (Picea glauca) and black spruce (P. mariana), birch (Betula) and alder (Alnus) in central Alaska during the interstade in mid-Wisconsin times, the climate subsequently became very severe, returning Arctic conditions in late-Wisconsin times. Spruce forests disappeared or were greatly diminished (Matthews 1974). There appears to be no evidence anywhere of any extensive stands from which a great thrust of boreal forest could have re-entered Canada from the northwest. There is also no evidence that any modern spruce species entered North America across Beringia in the Pleistocene or the Pliocene or that any spruce species entered Siberia from North America in this period. There are no white spruce or black spruce anywhere in Siberia or other parts of Asia and there are no P. obovata, P. jezoensis, P. koraiensis, or other Asian species in North American forests. The flora of Beringia in the late Quaternary was essentially that of tundra (Hopkins 1967).

Further inference that the Yukon corridor was utilized by forests migrating northward and not southwards is that there is currently no fir (Abies), apart from a few stations of amabilis fir (A. amabilis) in southeastern coastal forests in Alaska today, and there is no evidence that there ever was fir in Pleistocene time in continental Alaska. Balsam fir (A. balsamea) reaches north-central Alberta from the east, and the range of its close relative, alpine fir (A. lasiocarpa), actually makes slight overlapping contact with that of balsam fir in northcentral Alberta. This species extends sparingly into the Yukon from the south, usually at high or moderate elevations, and not reaching the Alaskan border. These firs over their whole ranges grow in association with spruce.

Figure 3 provides an illustration of Pleistocene occurrences of spruce and spruce-fir forests at full glacial and at late glacial periods down to the present Holocene period. Several groups of points may be noted, particularly those on the continental shelf off the coast of New Jersey extending upwards through George's Bank towards Nova Scotia and southwards past Nantucket to Virginia; those in west Texas near the panhandle and northwards along the eastern slope of the Rocky Mountains; and also points in Louisiana and southern Texas. As palynological data continues to be presented, particularly from the northern Great Plains, it becomes evident that there was spruce-fir forest rather continuously all across the whole ice front, extending from the Rocky

Figure 2. North America during full glaciation. Southernmost line represents the maximum extent of ice sheets about 18,000 years ago. Gray area represents ice margin at about 13,000 years ago (Canada 1973).

Mountains and onto parts of the exposed continental shelf of the eastern seaboard. This is not to say that there was a solid, deep spruce-fir forest, only that the type of forest that we have now in the boreal - jack pine (Pinus banksiana) and spruce, as well as fir in the east with extensive areas of fire origin poplar (Populus), and on some landtypes white birch (Betula papyrifera) - extended continuously from west to east in front of the ice. The forest that was present then looks relatively similar to that extant now in the boreal forest from northern Alberta through Ontario to Quebec. This forest was essentially simply displaced southward (Watts 1970; Wells 1970; King 1973). Stand variation, age and composition were related to successional development and site types just as our modern forest is today.

In addition, fossil mammal remains from the Great Plains to New England and the coast indicate that there were many boreal animals including musk-ox as well as several small mammal species from the modern fauna much farther south (King 1973). Also there were species of wooly mammoth (Mammutus sp.) and a wide ranging species of mastodon (Mammut americanum). At one time, mastodons were thought to be exclusively browsers, entirely restricted to spruce forests. More recent information suggests they were utilizing both wooded parkland and boreal forest (King 1973). Wooly mammoths were grazers and browsers feeding on tundra grasses, sedges, and conifer foliage such as spruce, fir and pine.

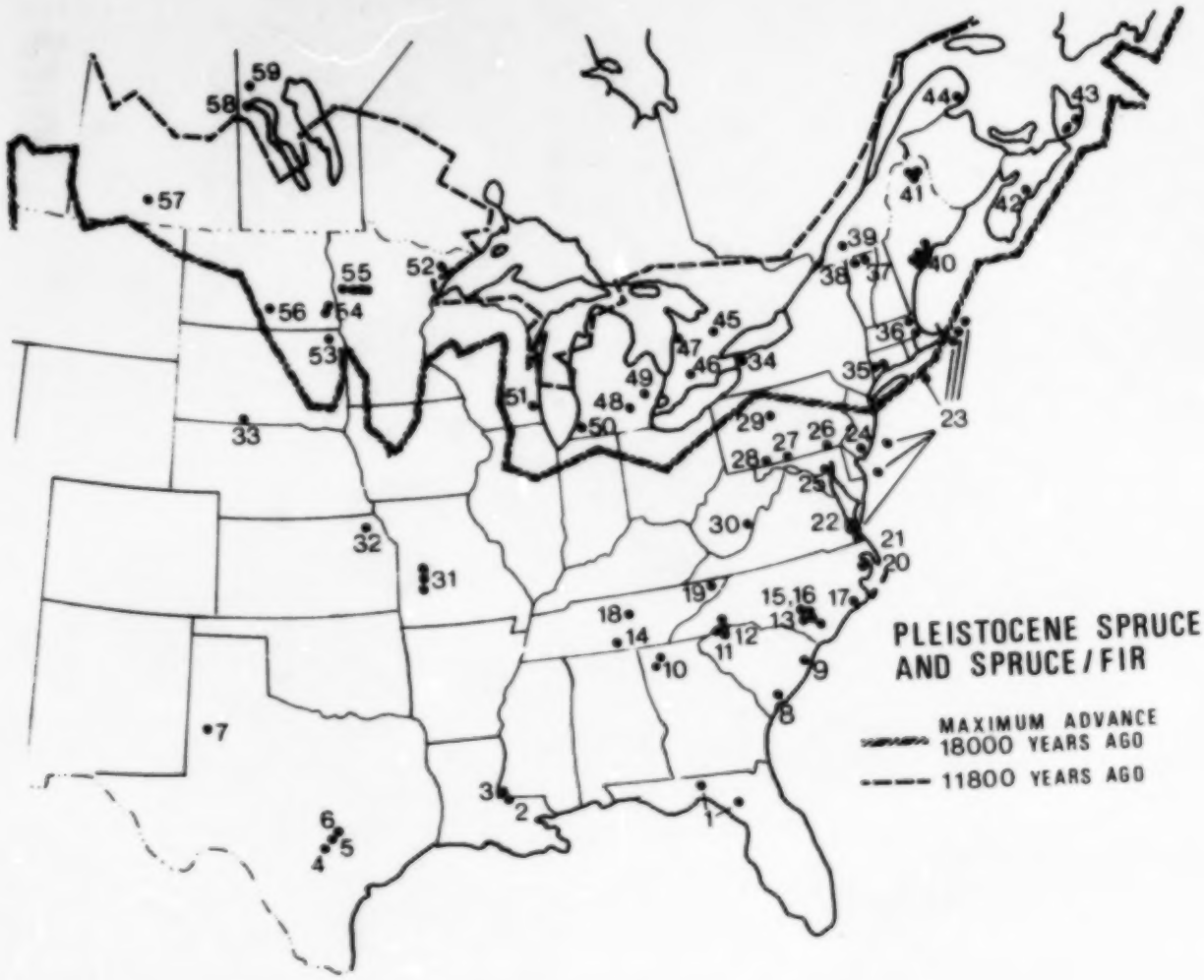

Figure 3. Pleistocene occurrences of spruce and spruce-fir forests at full glacial, late glacial and postglacial periods down to the present Holocene.* Locations: 1. Davis 1946; 2. Brown 1938; 3. Delcourt and Delcourt 1977; 4. Potzger and Tharp 1947; 5. Potzger and Tharp 1954; 6. Graham and Heimsch 1960; 7. Hafston 1961; 8. Leopold 1959; 9. Frey 1952, 1955; 10. Watts 1970; 11. Whitehead and Barghoorn 1962; 12. Cain 1944; 13. Whitehead 1967; 14. Delcourt 1979; 15. Barclay 1957; 16. Frey 1951, 1953; 17. Davis 1963; 18. Delcourt 1979; 19. Buell 1945; 20. Whitehead 1963; 21. Whitehead 1965; 22. Terasmae (in: Harrison et al. 1965); 23. Emery et al. 1967; 24. Potzger 1945; 25. Knox 1962; 26. Martin 1958; 27. Martin (in: Guilday et al. 1964); 28. Schrock 1945; 29. Sears 1935; 30. Darlington 1943; 31. King 1973; 32. Horr 1955; 33. Watts and Wright 1966; 34. Miller 1973; 35. Leopold 1956; 36. Davis 1958; 37. Miller and Thompson 1979; 38. Davis 1965; 39. Terasmae and Lasalle 1968; 40. Potzger and Friesner 1948; 41. Deevey 1951; 42. Livingstone 1968; 43. Livingstone and Estes 1967; 44. Livingstone 1968; 45. Terasmae and Matthews 1980; 46. Mott and Farley-Gill 1978; 47. Anderson 1979; 48. Andersen 1954; 49. Stoutamire and Benninghoff 1964; 50. Potzger 1954; 51. Wilson 1936; 52. Cushing 1967; 53. Watts and Bright 1968; 54. McAndrews 1969; 55. McAndrews 1967; 56. Moir 1958; 57. Ritchie and DeVries 1954; 58. Nichols 1969; 59. Nichols 1969. *Map modified after Stalker (1977).

Their remains have been found in Missouri, Michigan, New England and other places (Stoutamire and Benninghoff 1964; Whitmore et al. 1967).

There were other forest discontinuities along the ice front, occasioned by cold local climates and topography. In New England, for example, there was extensive tundra (Davis 1969). In the southern United States modern interpretation indicates that many southern hardwoods had compressed ranges, and here and there, in different kinds of niches, there was good survival of many Appalachian species (Watts 1970; Delcourt and Delcourt 1977). In the southern Appalachians migration is a little more complex. Early records indicate that the most logical interpretation is that both black and white spruce and jack pine extended southward on both sides of the Appalachian Mountains (Watts 1970).

There were two peaks of spruce, however, and one possible explanation is that the second peak in spruce in the late glacial (Leopold 1956; cf. Terasmae and Lasalle 1968) may have been the expansion of red spruce (Picea rubens) in some areas (Gordon/Leopold 1970, pers. comm.) closely followed by hemlock (Tsuga canadensis) (Potzger and Friesner 1948; Davis 1969). Many of these red spruce sites are not far from current areas of red spruce at higher elevations and in the Maritimes.

While pioneering chronological studies lacked good comparisons with sites of modern pollen rain, studies in more recent times have included comparative modern pollen rain data (Webb 1974) from similar but more northern sites. Correlations have been made, for example, between palynological sites in New England and northern Quebec (Davis 1969); Missouri with Great Lakes and eastern Canadian sites (King 1973); as well as comparisons with standing basal area (Leopold 1964).

As might be expected, there have been some interesting and fairly universal misinterpretations. A number of palynologists have shown that some sites located on the Great Plains indicated the presence of ash (Fraxinus) along with spruce in the pollen record and stated that no such stands were extant today (Baker 1965; Lichti-Federovich and Ritchie 1965; Cushing 1967; McAndrews 1967; Davis 1969; Gordon/Leopold 1970, pers. comm.). The interpretation of this and other observations (e.g. Artemisia and Picea) and even paleontological assemblages such as walnut and spruce led palynologists and paleobotanists to think that such species assemblages had no modern analogues, or that in a paleontological sense, some species had changed their ecological characteristics. In fact, there is no evidence that they have. These species have certain kinds of morphologies which are predicated on selection for certain ecological environments. They are unlikely to keep morphological characteristics constant through great ages of time if they have also been constantly changing their physiological tolerances. The unfamiliarity with species' site tolerances and requirements and with the present boreal forest itself, has also been misleading. In fact, there are a number of places in the north where white spruce does grow in proximity to black ash (Fraxinus nigra)! Figure 4 illustrates such a stand in the boreal forest of northern Ontario. The ash are growing in a site we call an ash flush about 120 m (6 chains) wide and about 0.8 km (0.5 miles) long. It is base rich - flushed with bases at higher concentrations than those of the surrounding physiographic sites. White spruce, balsam poplar (Populus balsamifera) and trembling aspen (P. tremuloides) occupy these adjacent sites. In this figure, a small lake is located in the immediate background. Any pollen rain studies from that lake would give substantial mixes of ash and spruce pollen together in the same diagram. It is a widespread but not a common phenomenon in the boreal forest, and is predicated on species requirements and edaphic limitations.

The soils of the Great Lakes, with their relatively high base status and consequently high pH, are not at all like the acidic granitic tills of the Canadian Shield. But, find occasional

Figure 4. An ash flush in the boreal forest, northern Ontario. The associated stands contain white spruce, balsam fir, trembling aspen, balsam poplar and some black ash.

pockets of like soils in the shield, and there is the species assemblage. Most of the sites from which chronological data is currently being collected have modern counterparts in stand composition and successional stage at a number of places in the current boreal forest or taiga.

The question arises as to how, for example, do we know, from the pollen record, a spruce was red, white or black in the mid-Appalachians. Early studies (Frey 1951) utilized some small differences in pollen size. There was size overlap, however, particularly in the pines, and some palynologists questioned the ability to separate such species as red pine (Pinus resinosa) from jack pine (Whitehead 1964) as well as to differentiate among the spruces with complete certainty. However, more recent studies (Birks and Peglar 1980) have identified other pollen characteristics, undulating cap margins, irregular reticulation in the sacci, etc. as well as the use of discriminant function analysis, all of which have enabled confirmation of earlier findings regarding Picea.

Arguments regarding, for example, the inability to separate pollen of red pine and jack pine due to size overlap did not take sufficiently into account those species' edaphic and climatic requirements and tolerances, their associated species and the presence of nearby macrofossils (cf. Whitehead and Barghoorn 1962; King 1973). When a pine species, red or jack, occurs with black spruce and such non-arboreal northern species as Myriophyllum farwellii, Lobelia dortmanna, Sanguisorba canadensis (Whitehead and Barghoorn 1962; Watts 1970) as well as Arceuthobium pusillum, the pine will be confirmed as jack pine rather than the temperate red pine.

A further point of interest has been the consistent presence of dwarf mistletoe (Arceuthobium pusillum) in the pollen record of the southern Appalachians (Whitehead and Barghoorn 1962) and as far south as Georgia (Watts 1970). Dwarf mistletoe, in host preference, is almost entirely restricted to black spruce. It does occur very rarely on red

spruce, although not presently in the southern Appalachians, and rarely on white spruce. During full and late glaciation, its consistent presence, along with black and white spruce and jack pine, suggests its association is most logically attributed to the boreal spruces.

The confusion among some palynologists with respect to the nature of the boreal forest may have been compounded by a number of phytosociological studies referring to north temperate montane and southern Maritime forests as 'boreal' when they were not. The floristics have similarities but differ in other respects. Still, in some recent literature, they remain described as 'boreal'!

At full glaciation, the boreal forest, dominated by jack pine growing on freely draining sandy plains, and accompanied by the boreal white and black spruces, reached northwestern Georgia (Watts 1970). In the late glacial in Louisiana (Delcourt and Delcourt 1977), southern Texas (Potzger and Tharp 1943, 1954) and probably northern Florida (Davis 1946) the boreal forest outliers were in fact just that. They were not part of a big continuous band of boreal forest extending down that far south, but rather outliers of the boreal such as one finds in parts of New Hampshire today.

Ecological Variation in the Spruce-fir Forest

For the purposes of this overview, a catalogue of phytosociological studies is avoided. Rather, examples of the principal types of spruce and spruce-fir forests are illustrated which demonstrate the wide ecological amplitude embraced by this forest.

The boreal forest or taiga is characterized by few arboreal species. In North America, the principal species are jack pine, which grows on pure stands or associated with black spruce and occasionally trembling aspen, white spruce which grows in cyclic association with trembling aspen or balsam poplar, and in the east, balsam fir. Eastern tamarack (Larix laricina) is widespread. Minor species include several species of alder (Alnus sp.), mountain ash (Sorbus sp.) and willow (Salix sp.). In the north this forest includes the spruce-muskeg as well as the spruce-lichen parklands and spruce ericaceous tundra ecotones; along the southwestern edge, the spruce-aspen-grass parklands; and in the east, enclaves of north temperate forest species.

What is the great spruce and spruce-fir forest like? In northwestern Ontario, white and black spruce are often associated together, along with balsam fir and aspen. This association also occurs in the Green River area of northern New Brunswick, but over much of their range, edaphic controls separate these species out more distinctly, balsam fir being frequently found growing in mixtures with white spruce or red spruce, but not black spruce.

Pollen records from Texas also indicate that, in the Pleistocene, fir grew more with white spruce than with black (Potzger and Tharp 1954). A point of interpretation about the pollen record is that the pollen of balsam fir is heavier than that of spruce, and while it does occur here and there in the pollen record, fir is usually under-represented (Davis and Goodlet 1960). Studies have been done to indicate that spruce pollen in the modern pollen rain is very closely representative of actual basal areas in the surrounding stands (Leopold 1964). Pines are usually much over-represented.

Figure 5 illustrates a subarctic spruce-lichen forest which occurs in the far north of Quebec, Ontario, Labrador and the Northwest Territories. Other associates which occurred earlier in post-glacial time have dropped out. There are great rock and outwash sand plains supporting lichen in a park-like forest which, depending on exposure and moisture regime, is intact in all the depressions. Such areas are much utilized by caribou for both food and shelter.

Figure 6 also illustrates a subarctic spruce forest. This is an upland forest with widely distributed black spruce with an ericaceous heath growing vigorously between all the trees. This forest is widely distributed from northern interior Alaska, across the Northwest Territories to Newfoundland.

A bit farther south - in parts of Alaska, the eastern Northwest Territories, northern Manitoba and Ontario on the Hudson Bay lowlands (Fig. 7) - the first closed boreal forest occurs, consisting of white spruce and aspen on the slightly higher eskers and postglacial beaches, while immense flats of small black spruce are found in the poorly drained intervening areas. These areas are often also associated with long string bogs, frequently without spruce, but rather, with eastern larch.

In interior Alaska (Fig. 8), successional stages of black spruce and ericaceous heath may be found at moderate elevations and following fire (Fig. 8, foreground). These stages are followed on north slopes by continuous and closed stands of black spruce (Fig. 8, background) (Viereck et al. 1983).

Figure 9 shows the south slope of the same area which is occupied by tall aspen, pure stands of white spruce, and mixed white spruce and aspen. The climatic delineation of these two spruces is dramatic in interior Alaska, the north slopes being almost entirely black spruce, and the south slopes largely white spruce (Viereck et al. 1983).

Stands of white spruce of magnificent form - tall linear-crowned trees - are very common in interior Alaska (Figs. 10, 11) (Juday and Zasada in press). The ground vegetation is feathermoss (Hylocomium splendens, Pleurozium schreberi, etc.). Such stands are also common in northcentral Quebec although they are generally considerably younger and are spruce-fir rather than pure spruce.

Figure 12 demonstrates gradual deterioration in interior Alaska. The tall white spruce decline. The stand gradually breaks up with no regeneration

Figure 5. Subarctic spruce-lichen forest (lichen tundra-forest ecotone) in northern Quebec.

Figure 6. Subarctic spruce-ericaceous forest (ericaceous heath tundra-forest ecotone) in northern interior Alaska.

Figure 7. Closed high boreal forest, Hudson Bay lowlands, Ontario. White spruce, aspen and white birch on eskers and beaches, black spruce on poorly drained flats, larch in the string bogs.

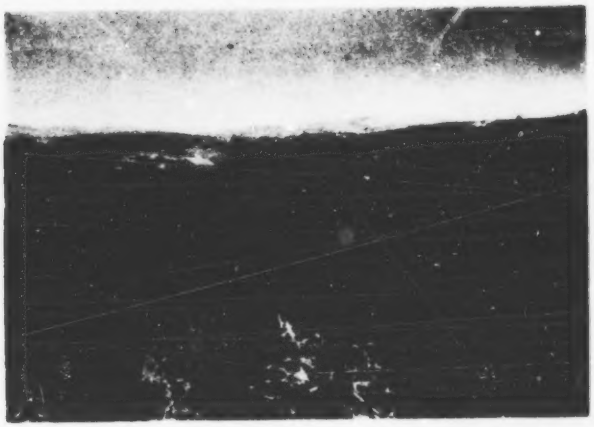

Figure 8. North slope black spruce, interior Alaska.

Figure 9. South slope white spruce and aspen, interior Alaska.

and black spruce commence to invade. This kind of stand transformation comes about through nutrient depletion on fresh or moderately drained floodplain sites or paludification on moist or wet sites. These are active processes in Newfoundland and Labrador, northern Quebec and Ontario through to Alaska. The black spruce succeeding on such sites usually become dominant for a rotation or so but are of low quality.

Figure 13 shows a black spruce ecosystem site in interior Alaska with an average age of 120 to 140 years (Viereck et al. 1983). Such stands are sometimes referred to as the 'drunken forest'. The trees are about eight metres high and of very small diameter. They are all leaning in various directions. Similar stands occur at the higher latitudes in northwestern Ontario.

The Green River area in northern New Brunswick is a typical closed boreal forest. Figure 14 demonstrates the massive catastrophic deterioration of white birch and the cyclic replacement by the spruce-fir forest coming up through it. This forest is now

Figure 10. Tall linear-crowned white spruce in interior Alaska.

Figure 11. Interior Alaskan long-boled white spruce; feathermoss floodplain site. Stand age up to 240 years.

Figure 12. Interior Alaska degraded white spruce site; black spruce beginning to invade.

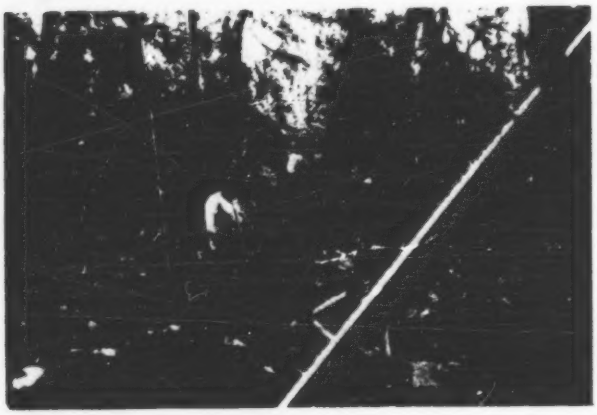

Figure 13. The 'drunken forest'. Mature black spruce growing over permafrost. Interior Alaska.

much more dominated by fir than in former times as a result of cutting and budworm spraying practices.

Where the boreal spruce-fir forest impinges on the north temperate forest the composition of the stands is frequently under edaphic as well as climatic control. Successional stages are also of influence as are the number of species involved and individual species tolerances.

Figure 15 shows such an area in the Algoma region of Ontario. Examples such as this are repeated endlessly across southcentral Ontario,

Figure 14. Green River, northern New Brunswick 1962. Catastrophic dieback of white birch. Rising regeneration predominantly fir with some spruce and white birch.

Figure 16. Red spruce-fir stand in a 'sea' of tolerant hardwoods, southcentral Ontario.

Quebec, northern Vermont and New Hampshire. This is a north temperate forest showing very tall white spruce and good balsam fir, surrounded by other sites which are supporting tolerant hardwoods. There is a ridge in t · background with hemlock and white pine (Pinus strobus). This kind of stand is common throughout northern New England. It could well have been the kind of stand that provided the pollen rain for the Louisiana sites during late glaciation, not large, but repeated over and over again with nearby associated hardwood areas.

Figure 16 shows a pure intact stand of red spruce and balsam fir in southcentral Ontario. It is encompassed by a 'sea' of tolerant hardwoods with a few conifers. This is very similar to southern

Figure 15. Algoma, central Ontario. North temperate boreal forest with white spruce and fir.

Figure 17. Northcentral Ontario, north temperate forest; hardwood niches in a 'sea' of boreal spruce and fir.

Appalachian stands today. When cooling glacial climates put pressure on temperate hardwoods, the areas they occupied would diminish and conifers would advance out across these hardwood areas. The hardwoods would persist in their own special niches, and to some extent in mixtures, but the general niche of the conifers would expand.

By moving northward two and one half degrees in latitude to the northern part of Algoma in north-central Ontario (Fig. 17), an idea of what that shift would have been like is provided. Here, it may be noted, is a great sub-boreal forest filling all the valleys and sweeping across the landscape. The 'sea' is now composed of mixed conifer stands. The tolerant hardwoods are confined to their niches here and there, and may be noted as light patches on the southwest - facing ecoclimatic sites on the upper slopes. The rest of the country is all boreal spruce and fir.

Moving westward, Figure 18 provides an example

Figure 18. Cypress Hills, southeastern Alberta sub-boreal forest: white spruce and lodgepole pine.

of what some of the boreal forest may have looked like on the Great Plains in the west. This is in the Cypress Hills in southeastern Alberta and southwestern Saskatchewan. These are pure white spruce and lodgepole pine (Pinus contorta) stands. This relatively small block of land is of moderate elevation above the general plain. It demonstrates that the local climate can hold sub-boreal forest here. On the nearby plain on a lower slope, there is another fragment of the same stand as well as examples of spruce-aspen parkland. These are modern stands, but during late glaciation, or presently, given any cooling climatic shift, this stand could expand from here and advance across the visible plains to join up with other stands at great distances. There are no other spruce in this particular instance within 280 km (175 miles), but this is clearly a glacial remnant. Pollen and macrofossil data indicate that such forests were widespread on the northern Great Plains (Wells 1970).

Figure 19. North temperate forest; white spruce-black ash flush, central Ontario.

Referring back to commentary on some of the palynological studies indicating that ash and spruce were not associates, Figure 19 provides an example in the north temperate forest of Ontario where black ash and white spruce are growing well together. Both species are tall, emergent trees. They are in a valley here surrounded by other forest types but the stand will repeat itself in this edaphically restricting site. The regeneration consists both of ash and spruce.

Information is accumulating on the nature of the postglacial migration of white spruce in eastern North America. The first of these is phytosociological data (Löve 1959) which showed that there is a separation of an eastern and western component of floristic associates of white spruce. One group, called the 'eastern boreal element', migrated in a northerly direction from the Great Lakes area into eastern Manitoba and around the north ends of the prairie lakes. A second group of plants, the 'western boreal element', invaded Manitoba from the west. Some members of this western group migrated as far east as James Bay. White spruce were associated with both of these migrations.

Holst (1960) from preliminary provenance studies was the first to suggest the possibility of two clines of white spruce from south to north, one east of the Ottawa valley and one west. Nienstaedt (1968) showed from available provenance material that the southeastern distribution of white spruce was in all likelihood a two-pronged cline extending into northwestern Canada on the west side of Hudson Bay and into Labrador on the east. These findings were further elucidated by Wilkinson et al. (1971) who showed, utilizing cortical oleoresin monoterpene composition of white spruce provenances, that there were indeed northeast and northwest aggregations in white spruce populations. The principal division occurred up the Manitoba-Ontario boundary to the northwest and eastwards to Labrador, similar to the inferences of Löve (1959). There was also a minor division from the southeast up the Ottawa valley.

The immensity of the range of white spruce provides the principal clue to the great ecological diversity and the related genetic selection embraced by this species. A number of ecologically distinct sites and associations, for example, shallow calcareous soils, and even northern alkaline swamps have not been mentioned in this overview.

The place of fir in the forest is also of prime importance. Balsam fir is a boreal species by origin - its prime centres in the east are in the Maritimes and parts of Quebec. Inventory data in Ontario suggests that relative to other species, it represents only a small percentage of softwood volume. It becomes a somewhat weaker competitor as it goes to the northwest in northern Manitoba and Saskatchewan. Its range sparingly overlaps that of its Rocky Mountain variant, alpine fir, in central Alberta (cf. Parker et al. 1981). The latter species, while fairly widely distributed in uplands of the Yukon, does not get into the main part of Alaska, although at high elevation it is present along with spruce and mountain hemlock

(Tsuga mertensiana) in coastal southeastern Alaska. Amabilis fir is mentioned previously.

Balsam fir in the northeastern forests is not nearly as long-lived as spruce and rots out much earlier. However, regardless of its volume as it approaches maturity, its regeneration is extremely aggressive, both in Ontario and eastwards, and much more so than that of spruce. There are always new and rising waves of fir regeneration in much of the northeastern spruce-fir forest. In parts of central and northern Maine and northcentral New Brunswick, it is near the centre of its biotic potential. The best stands of almost pure fir which occur in Quebec and northern New Brunswick might give the impression that this is predominantly what that country has produced. However, historical accounts of much of this area indicate that enormous volumes of spruce have been cut out there in the past, e.g. in the Miramichi area (Longley, D. 51, 1962, pers. comm.). The forests have experienced a marked shift as a consequence of man's activity and in the face of the much more successful regeneration capabilities of balsam fir.

In the Adirondacks (Adams et al. 1920) and in the northern Appalachians, pure balsam fir on the upper slopes of the higher peaks represents a true boreal forest above the temperate montane red spruce, and red spruce-balsam fir mixtures on the midslopes. These balsam fir forests replace themselves through a process described as fir waves. All the trees in an elevational band reach natural rotation age and die about the same time. Regeneration commences in the openings and the whole wave gradually advances upslope in the direction of the wind flow (Sprugel 1976; Sprugel and Bormann 1981). Above the fir forest there may also be scrubby balsam fir and, higher up, black spruce krummholz such as one finds on Mount Katahdin, Mount Marcy and Mount Washington (Löve and Löve 1966).

In the southern Appalachians, balsam fir intergrades with fraser fir (Abies fraseri) (Robinson and Thor 1969), an endemic species of high elevation in the south. Red spruce and fraser fir both have temperate montane characteristics: for example, flushing much later than does balsam fir.

The Productivity, Structure and Functioning of the Spruce-fir Forest

Differences in productivity related to shifts in latitude and to differences in site and forest type are presented in Table 3 (Gordon 1983). In the eastern boreal forest, a very common condition of white spruce stands is that they are usually mixed with balsam fir and white birch, or with aspen. Stands may be pure conifer or mixedwood. The two white spruce mixedwood stands, which are still carrying the shorter-lived species, are on different sites accounting for dry matter productivity differences between 4,742 and 5,755 kg $ha^{-1}year^{-1}$. While these mixedwood sites are quite different from the black spruce sites, the productivities are equivalent. The latter are both Site Class 1 black spruce stands (Plonski 1956).

Table 3. Aboveground productivity (litterfall plus increment) in kg $ha^{-1}year^{-1}$ for five spruce and spruce mixedwood stands.

Lat.	Site	
45°30'N	Red spruce mature - fresh till	8703.7
46°42'N	Black spruce immature - fresh outwash sand	5742.3
49°15'N	Black spruce mature - moist peat	4568.3
49°12'N	White spruce Mixedwood mature - fresh-moist silt, fine sand	5755.0
49°33'N	White spruce Mixedwood mature - fresh till	4742.4

Black spruce also grows, however, on wetter sites than these highly productive sites, and as moisture regime increases (gets wetter), productivity of black spruce decreases. Red spruce stands on the fresh till are much farther south in the north temperate forest and have a higher productivity reflecting better climate. These are measures of very productive forests of spruce and spruce-fir types on sites on their respective moisture catenas. At lower site classes at these same latitudes there would be much lower productivity.

Figures 20 and 21 (Gordon 1983) present examples of nutrient cycles in a north temperate red spruce stand and in a boreal white spruce mixedwood stand. The structure and functioning of these stands are somewhat similar so the cycles are expected to be more similar to one another than they would be to that of other species such as pure hardwood stands or other conifers. There are some differences, however, which are a consequence of the differences in the nutrient status of the sites on which these types grow. Red spruce stands are normally found on more acidic sites than those on which white spruce mixedwood would grow. This red spruce stand is predictably more acidic: compare calcium levels in the reserves - for red spruce 399 kg ha^{-1} vs. 1918 kg ha^{-1} for white spruce mixedwood. More rapid turnover rates are expected in the white spruce mixedwood and more accumulation in the red spruce stand. For nitrogen in the red spruce stand, there is more than one and a half times as much nitrogen in the reserve components as there is in the white spruce mixedwood. However, the amount of nitrogen being cycled as exemplified by uptake is approximately the same.

Both phosphorus and magnesium have substantially greater amounts in the reserve components of the white spruce mixedwood than in the red spruce and this is reflected in the lower amounts involved in uptake in the red spruce stand. These amounts are, nevertheless, sufficient for adequate growth in a less demanding species like red spruce. In the case of calcium, the white spruce has five times more in the reserves than that of the red spruce and yet strangely, the amount of calcium cycling in the red spruce is nearly equivalent to that of the white spruce mixedwood.

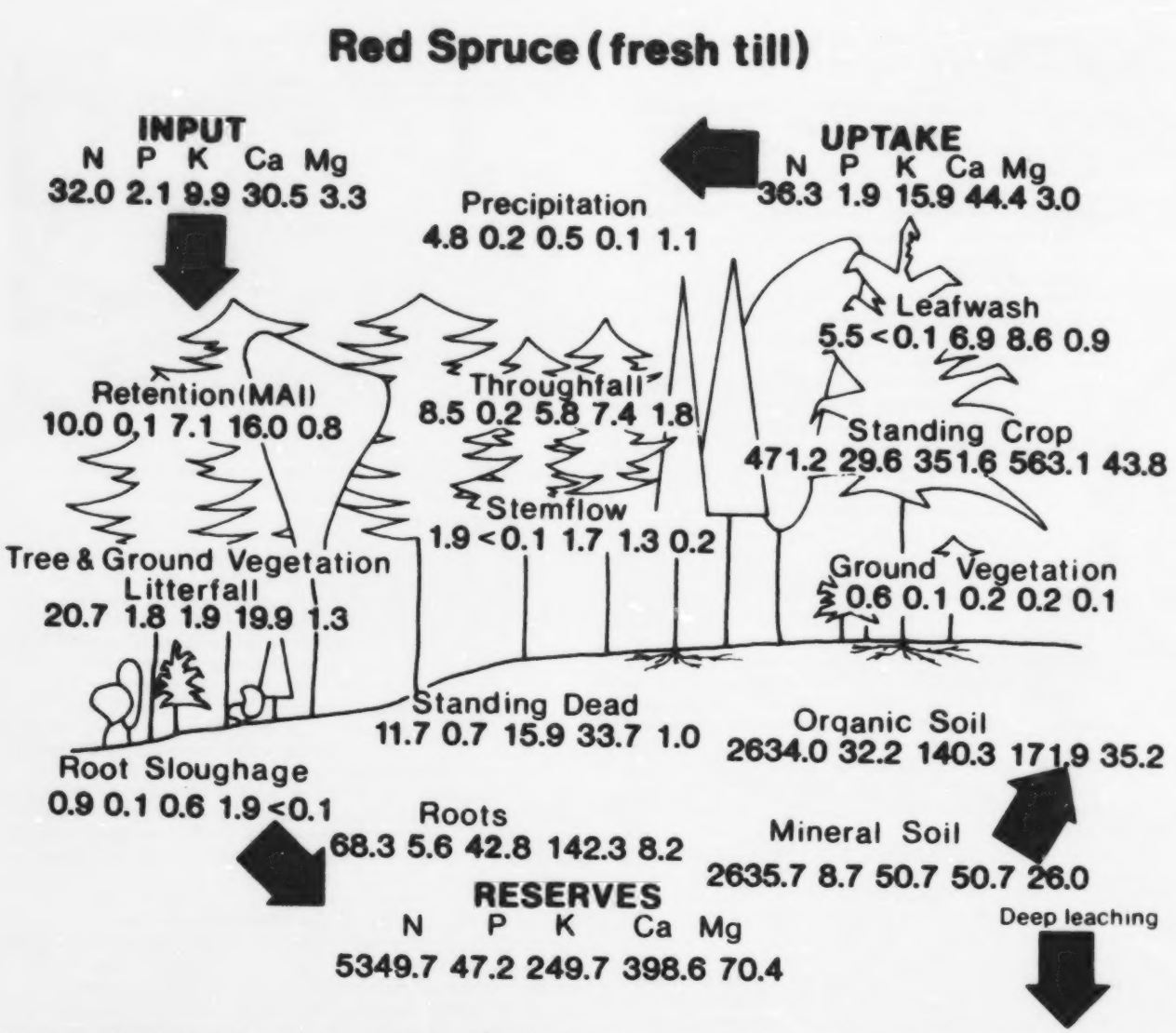

Figure 20. Stylized nutrient cycle (kg ha^{-1}) of a north temperate red spruce forest on fresh granitic till. Species represented are red spruce, balsam fir, eastern hemlock, yellow birch and sugar maple.

For potassium, the amounts in the reserve components are about the same in both stands but the red spruce are getting by with about two-thirds of that of the more demanding species in the white spruce mixedwood stand. Incidentally, balsam fir are present in both of these stands.

Evolution of the Genus Picea

The evolution of the genus Picea and more particularly the origin of white spruce is important since it is the principal and constant constituent of the boreal spruce-fir forest of North America. As recently as 1955, and even later, Beringia, which was exposed off and on from the mid-Pleistocene at least to mid-Wisconsin time, was considered to be the likely route through which spruce entered North America and diversified. At the same time, it was well known to many paleobotanists that there were fossils dating back to much earlier times through the Tertiary in a number of places in North America. As the reality of continental drift (Melville 1966; Wilson 1966) began to become more widely accepted in the late '60s, it became evident that the advent of Picea into North America had indeed taken place much earlier in the Tertiary or even the Cretaceous (65 million years ago) before continental drift had isolated North America (Gordon 1968).

It is generally accepted that conifers originated before the angiosperms (Florin 1963; Sneath and McKenzie 1973) and that the latter were indeed very common in the Cretaceous period. Spruce-like fossils are very rare, however, in that period although pine fossils are fairly common. There are at least two reasons that there are few examples

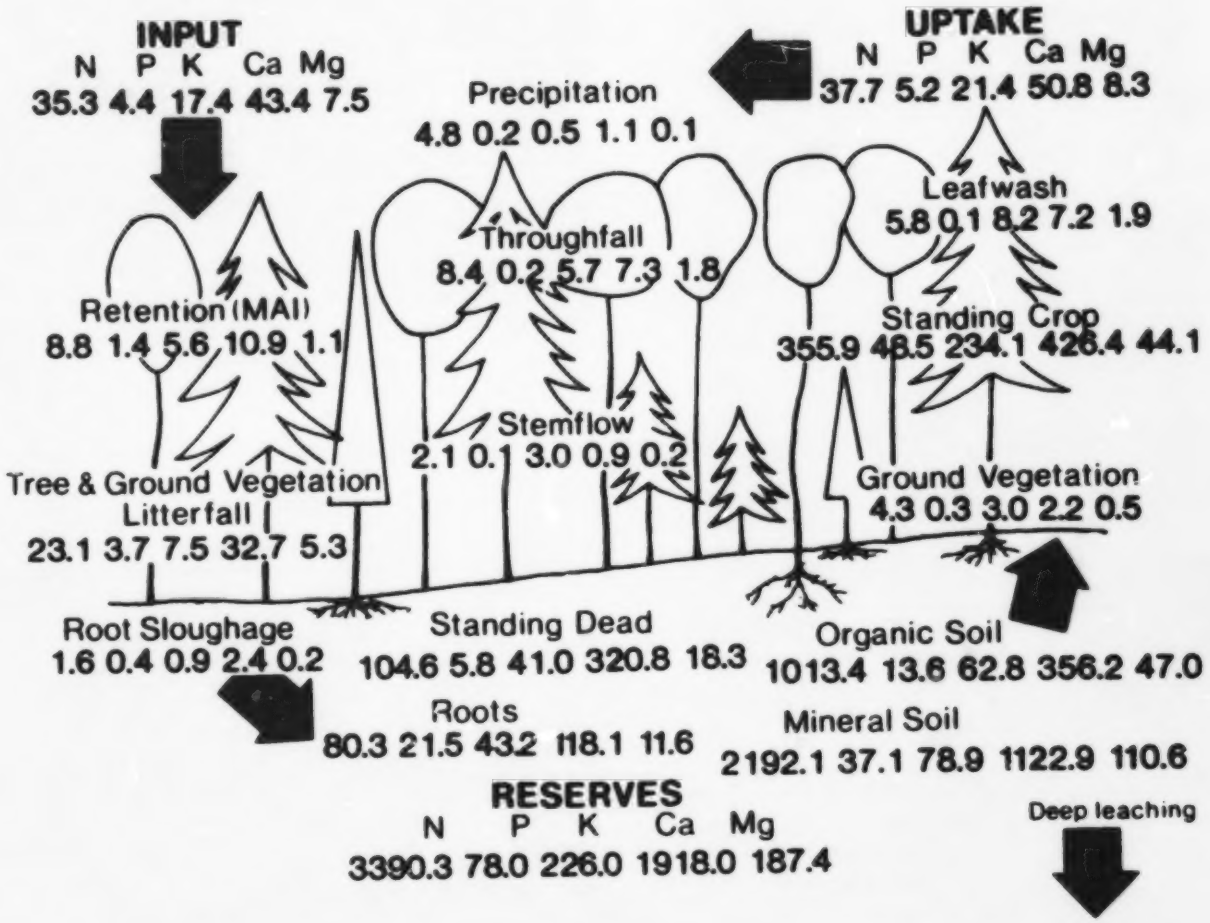

Figure 21. Stylized nutrient cycle (kg ha^{-1}) of a boreal upland mixedwood on silt, fine sand. Species represented are white spruce, balsam fir, trembling aspen and white birch.

of Picea from the Cretaceous. Their origin and radiation from the Pinaceae may not yet have occurred (Miller 1976), and just as likely, the sites on which Picea grew were mostly upland and not near good sites of preservation.

Miller (1976) very thoroughly evaluates early fossil Pinaceae from the Cretaceous and onwards. Floral or fruiting parts of plants are the most constant attribute through time in fossil evaluation. An extremely small number of traits (one or two) involving the number and configuration of resin canals in cone scales of conifers, so far has proven to be of high diagnostic value in relating fossil specimens to different species and genera. The small number of Cretaceous spruce-like fossils thus far found in North America has been disqualified as Picea, and assigned to other extinct genera, although fossil Picea specimens have been obtained from the late Cretaceous in Europe. It is generally accepted that late Cretaceous thus far represents the age of the genus.

The flora of the northern hemisphere has been essentially modern since the Pliocene (about 11 to 2 million years before the present) and have come down to us from that period through the Pleistocene to the present with very little change. More precise information as to when species arose, separated or diversified would aid in our understanding of taxonomic relationships and chemical and genetic bridges and barriers that are being encountered in breeding work. Many of the species involved are from different continents which have been separated for very long periods of time. This understanding, in turn, helps greatly in developing tree improvement strategies.

In the case of North American native spruces, white and black spruce are both modern species. There are no fossils older than the Pleistocene and Pliocene. Red spruce on the other hand appears

Figure 22. Fossil Picea banksii cones from the late Miocene. Banks Island, northwest Canadian arctic (Hills and Ogilvie 1970).

to be an older species. It grows with flora known as the Arcto-Tertiary flora and has been associated with that flora for a very long time, well back into the Tertiary period. It has affinities with a number of older Eurasian species (Gordon 1976). Many other hardwood species in the southern and central Appalachians have occupied and have been migrating up and down the Appalachians throughout the Tertiary period and since.

Genecologists, in common to some extent with paleobotanists, look upon new and old species as having different attributes. One of these is that in general old species, e.g. Ginkgo, Liriodendron, tend to have no, or fewer, enemies than new species or they have come to terms with those that they have (Wright 1955). Young species tend to have a wider array of pests or enemies and these often occur in epidemic proportions. Also, old species tend to have shrinking ranges.

Apart from common Juniper, and its co-Pleistocene companion species, black spruce, white spruce has a range far greater than any other North American conifer. None other of the Pinaceae have ranges which are anywhere near as large. Its range is much greater than its associate balsam fir. Its present range is with few exceptions restricted to landscapes which have been glaciated. No fossil counterparts extending back beyond the Pliocene have been located as yet. Its closely-related montane counterpart is Engelmann spruce (P. engelmannii) with which it freely hybridizes. This species however has a fossil counterpart, P. lahontense, which is known from a number of sites in Idaho, Oregon and Colorado, back through the Miocene and Oligocene epochs from approximately seven to thirty-eight million years before the present.

One other interesting possibility is P. banksii (Hills and Ogilvie 1970), a fossil species from the late Miocene (Fig. 22). Some of the cones of this species, however, are quite different from those of modern white spruce. White spruce, incidentally, both now and in the Pleistocene (Brown 1938) has cones which vary greatly in size between provenances and occasionally between families (Gordon, unpubl.). Incidentally, the associates of P. banksii were in general those of an eastern mixed forest, equivalents of jack pine, white pine, eastern hemlock, larch, alder, hazel (Corylus), butternut (Juglans) (Hills, L.V. 1969, pers. comm.) such as might be observed in parts of southcentral Ontario today.

Genecology in White Spruce

White spruce shows astonishing variation in crown form. Crown form, doubtless acquired through this species' long migrations as a consequence of the different environments and associates, is now regionally centred. Northern types tend to have crowns which are more linear and columnar; southern ones are usually more broad-crowned.

The important selection pressures would relate to whether or not this species grew in pure conifer stands of spruce or spruce-fir, or in mixtures with hardwoods, such as trembling aspen and white birch or tolerant hardwoods. There would likely be, for example, greater selection for broader crowns among those growing with hardwoods. Similarly, selection pressures would exist relating to whether snowfall was wet or dry, heavy or light; broad-crowned types tending to take the strategy of being able to hold snow up without breakage, narrow-crowned types tending to shed it. While narrow-crowned types do tend to be more uniformly distributed at higher latitudes, there are small populations of tall, narrow-crowned spruce existing as isolates at lower latitudes in the spruce range.

There are also several different types of crowns within the narrow and broad groupings. For example, Figure 23 shows an uncut face of a white spruce stand in Alaska. Of the crowns clearly visible in this picture, all but two are extremely narrow-crowned types, typical of interior Alaskan crowns. Two of them are somewhat broad relative to the others, but by southern standards, not broad.

Figure 24 illustrates an unusually narrow-crowned tree in central Ontario. This crown is sufficiently narrow that some would identify it as black spruce.

Very tall, narrow linear crowns of central Alaskan white spruce are shown in Figure 25. These crowns are so narrow that it leads less experienced people to call them hybrids of white and black

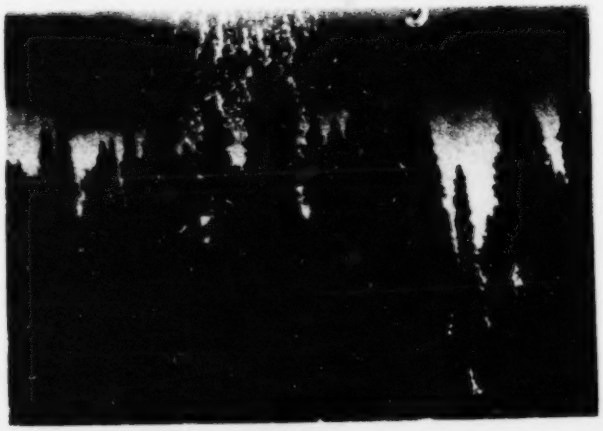

Figure 23. Interior Alaskan white spruce, tall narrow columnar-type crowns.

spruce or even simply black spruce.

A typically broad-crowned type is shown in Figure 26. This is in Site Region 5 of central Ontario in a north temperate forest. This type is very common in New Hampshire and central Maine. This crown type in Norway spruce is known as bürsten-fichte (Priehäusser 1958).

Figure 27 illustrates a broad, pendant-type crowned tree from central Ontario. All the twigs

Figure 25. Long narrow linear crowns of mature white spruce, interior Alaska.

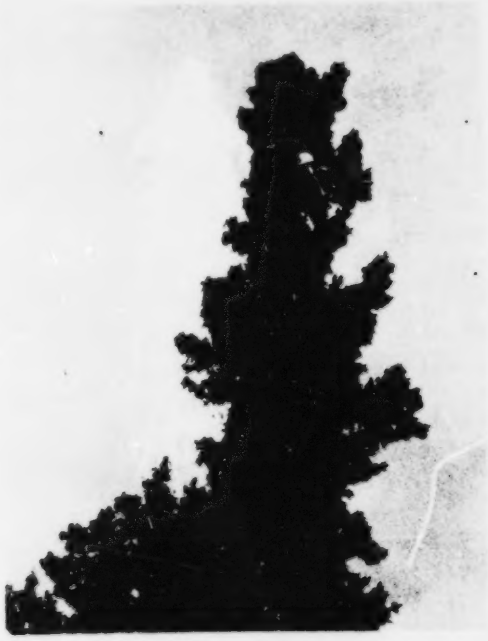

Figure 24. Unusually narrow-crowned white spruce, central Ontario.

Figure 26. Broad-crowned white spruce, north temperate forest, central Ontario.

Figure 27. Broad pendant-type crown, north temperate forest white spruce, central Ontario.

Figure 29. Long linear-crowned, highly productive white spruce, central and northern Ontario.

Figure 28. Spike-type, north temperate forest white spruce, central Ontario.

Figure 30. Pollen collection in superior white spruce.

on this tree hang down. There are first and second order branching, but the second order branching is all pendant. More extreme forms of this crown type are commonly found in Norway spruce and are known as Kamm-fichte (Priehäusser 1958). This tree is broad-crowned and is growing with tolerant hardwoods and hemlock in a north temperate forest.

A 'spike-type' crown is shown in Figure 28. The bole is long and linear with a very narrow taper. There are first order branches going out from the bole but essentially no second order branches at all. There are many small third order twigs growing from, and pointing in all directions from, the first order branches. The crown has an excessively see-through appearance. This crown type also occasionally occurs in Sitka spruce (P. sitchensis).

Figure 29 illustrates a tall, linear-crowned tree, occurring in central and northern Ontario. It would be classed as a rather narrow-type crown but would be still broader than those in central Alaskan trees. This tree is a very desirable type for tree improvement work. Its height-to-diameter ratio is excellent: a long, linear tree with excellent crown form. Figure 30 shows pollen pickers at work in that tree.

With such wide variation in species such as white spruce, genecological questions such as the crown-type strategy are of considerable importance in breeding and tree improvement. These different strategies relate markedly to efficiency and productivity.

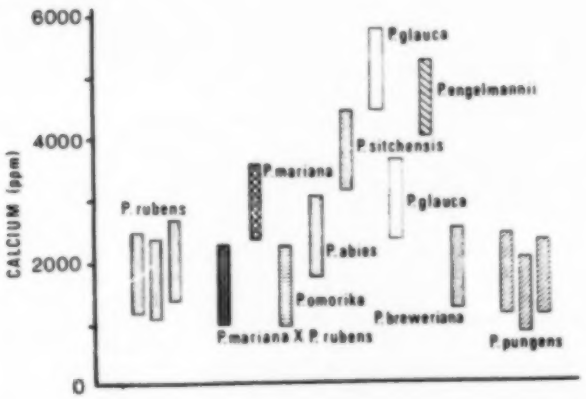

Figure 31. Calcium uptake of different spruce species and family sources, growing on a common, low lime landtype.

Another genecological consideration is nutrient uptake. Figure 31 illustrates calcium uptake in a number of species and family sources of spruce. For the sake of argument, they could be called 'genotypes' of the genus. These trees are growing in replicated plots in a Picetum in southcentral Ontario at latitude 45°30', and are all on the same landtype. The landtype is a deep fresh granitic till and moisture is not limiting. However, the only source of calcium is the granitic petrography, and lime concentrations in the soil are not high. The different patterns of calcium uptake exhibited by various species groupings are of interest. Three populations of red spruce on the left are relatively similar. A black x red spruce hybrid family population is not different from red spruce, yet the uptake of calcium by a pure black spruce population is significantly greater than that of red in all but one population.

Serbian spruce (P. omorika), in its native sites in Europe, grows on limestone benches in the Dinaric Alps. In this Picetum, like red spruce, it is not taking up much calcium. This species may have a method of controlling calcium uptake or it may simply reflect the low calcium availability of this landtype. Calcium uptake in Norway spruce (P. abies) is a little greater but not essentially different from that of red. Blue spruce (P. pungens) and Brewer's spruce (P. breweriana) are at the same general level as that for red and Serbian. None of the populations of these species are taking up very much calcium, either demonstrating an ability to exclude it or the fact that it isn't available in the first place.

However, when the uptakes of Sitka, white and Engelmann spruces are considered, calcium availability does not appear to be limiting. There are two families of white spruce, one of them clearly taking up substantial amounts of calcium, even though lime supply in this landtype is not high. This is true for Engelmann spruce, and Sitka is not far behind. A second population of white spruce has lower uptake, about the same as for black spruce, but still in general greater than that of red, Serbian, blue and Brewer's spruces. Differences in uptake also are apparent for other elements not shown here (Gordon, unpubl.) demonstrating marked species differences in tolerances and uptake. This accounts to some degree for the exclusivity of some species growing on certain kinds of sites, and the more universal edaphic distribution of other species and populations within those species.

Nienstaedt and Teich (1972) have provided an excellent review of the genetic status of white spruce. Essentially, where white spruce comes in contact with Sitka spruce on the Kenai Peninsula of Alaska, and in the Skeena River Valley of B.C.; and where it comes in contact with Engelmann spruce in British Columbia, Alberta and Montana, there are extensive areas of introgressed populations of these species. Accounts of possible introgressive hybridization or even casual hybridization between white spruce and black spruce (Larsen 1965; Roche 1969) are unfounded, and are in sharp contrast to all artificial crossing information. A crossing table modified from Nienstaedt and Teich (1972) follows.

Table 4 sets down five categories of cross compatibility of white spruce with other North American and Eurasian spruce species. Introgression between Engelmann and Sitka spruce has already been mentioned. Crossing is relatively easy with Yeddo spruce (P. jezoensis), a Japanese species of two varieties. This species is somewhat similar to Sitka, but it differs from it in a number of characteristics and does not have the growth

Table 4. Cross compatibility of Picea glauca and other Picea species

Easy	Moderate	Difficult	Very Difficult	Failure
[1]P. engelmannii+	[4]P. pungens	[8]P. likiangensis	[11]P. mariana ⟷	P. mariana
[2]P. sitchensis +	[5]P. schrenkiana	[9]P. mexicana	[12]P. rubens	P. chihuahuana*
[3]P. jezoensis	[6]P. smithiana	[10]P. maximowiczii	P. koyamai ?	P. purpurea
	[7]P. omorika		P. koraiensis?	P. balfouriana
			P. bicolor ?	
			P. wilsonii ?	
			P. orientalis?	
			P. glehnii ?	
			P. abies ?	
			P. asperata ?	
			P. meyeri ?	
			P. montigena ?	
			P. retroflexa?	

+Also introgression

*Consistent failure

?Hybrid reported by one worker, but attempts by all other workers have consistently failed (hybrid still unverified)

First successful crosses are indicated: 1. Larsen 1948; 2. Eklundh 1943; 3. Rehder 1967; 4. Wright (in: Santamour 1967); 5. Fowler 1966; 6. Fowler et al. 1976; 7. Oksbjerg 1953; 8. Jeffers 1971; 9. Gordon 1980; 10. Jeffers 1971; 11. Gordon 1980; 12. Bongarten and Hanover 1982.

characteristics of Sitka.

The second category, moderate, has four species in it. These are species with which successful crosses are possible but not with all clones, and in which there are some barriers. If they are open-pollinated, side by side, crossing is very infrequent, but may be accomplished artificially with some effort.

The third group, classed as difficult, are species which can be occasionally crossed with some clones, but there have been many attempts at artificial crossing which have not been successful.

The fourth, or very difficult, category are those species which have been crossed very rarely with white spruce. Only one or two workers have been able to cross white spruce with red. Other species in this list are very uncertain. Hybrids have been reported but there has never been any verification of any of them. In general, white spruce does not cross with Norway spruce, or its close relatives, P. asperata, P. meyeri, P. montigena and P. retroflexa. There has possibly been one artificial cross made between black spruce and white spruce, and there is one individual occurring in nature called the Rosendahl spruce (P. glauca x mariana) which is so far considered to be the only possibly legitimate example of a putative natural hybrid. Most consistently, failures have been endless in attempting to cross white spruce with the four species listed in the last column. However, several of those in the very difficult category could probably be legitimately moved over to the last column.

The information generated from work on hybridization is being used in studies elucidating incompatibility, embryo inviability, hybrid inviability, crossability, homo and heterozygote phenomena, backcrossing phenomena, crossing frequency, ecological barriers, homeostasis, introgression, gene flow, genetic behaviour of sympatric and allopatric populations, genetic drift, genetic distance, heritability, quantitative population and ecological genetics, and many phases of tree improvement, wood quality, genotype x environment interaction, selection, propagation, etc.

Stand Dynamics of the Spruce-fir Forest and the Budworm (Choristoneura fumiferana)

The following stand structure and dynamics data (Figs. 32-38) illustrate and compare typical white spruce-fir stands in the boreal forest and typical red spruce-fir in the north temperate forest and show how the perpetuity of the spruce component in such stands is related to budworm events. The white spruce-fir example is in north-central Ontario, latitude 48°00', longitude 82°30', elevation 366 m; the red spruce-fir example in southcentral Ontario, laticude 45°00', longitude 77°18', elevation 335 m. The data are based on a series of plots in areas that have had the customary historical budworm events of most eastern spruce-fir forests.

Figure 32 presents primary stand structure of the white spruce-fir forest. At this stage of development, there are typically low numbers of very large white spruce trees. There are moderate numbers (20 per hectare) of immature trees in each centimetre class between 10-20 cm, and fairly good numbers (200-50 per hectare) in the 5-8 centimetre classes, respectively. Fir, in contrast, have no trees greater than 15 cm. However, in the 5-8

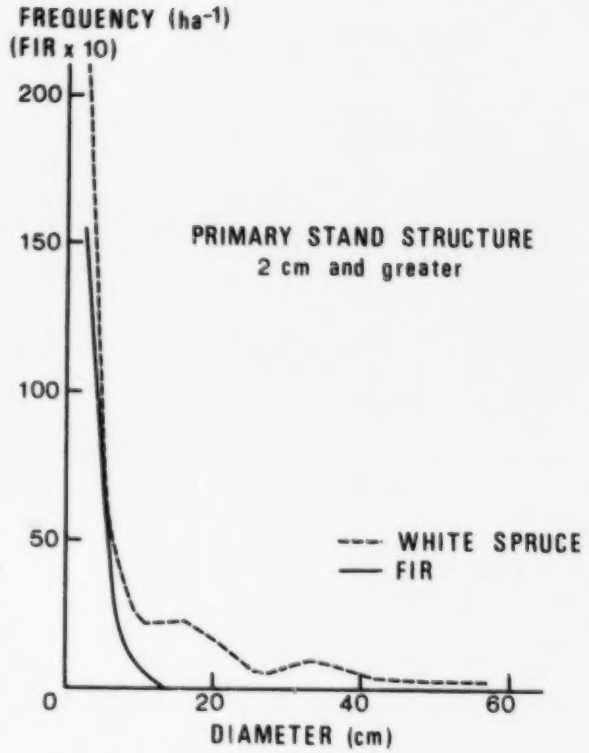

Figure 32. Primary stand structure, white spruce-fir.

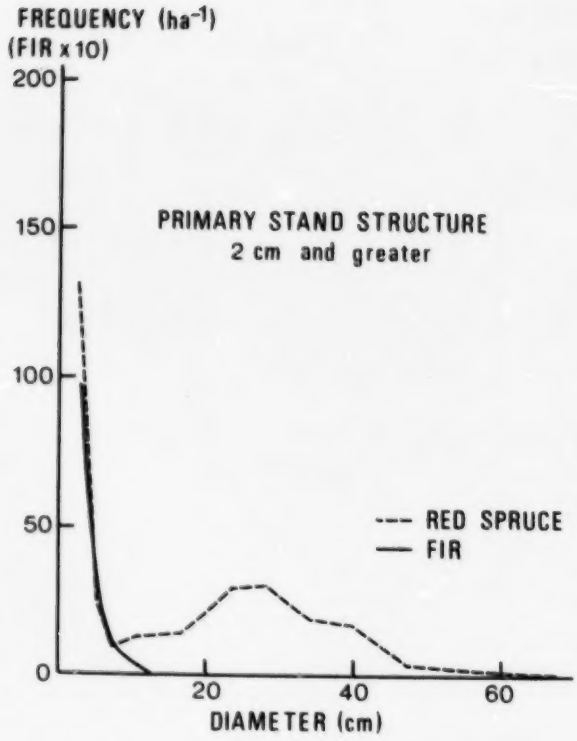

Figure 33. Primary stand structure, red spruce-fir.

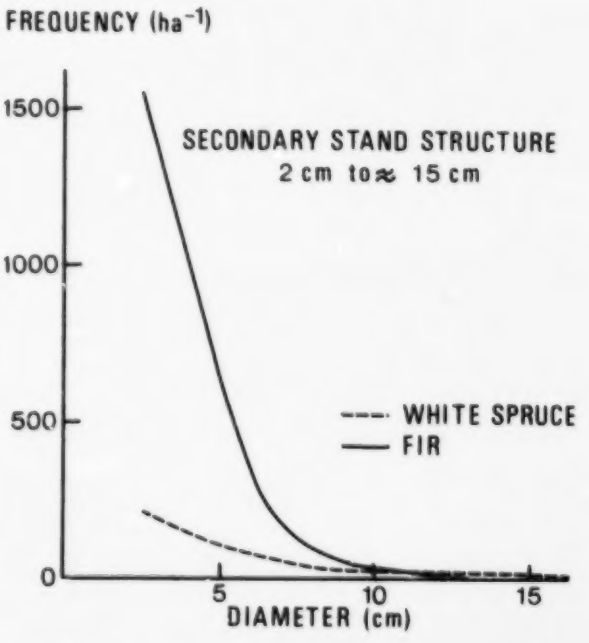

Figure 34. Secondary stand (rising understory) structure, white spruce-fir.

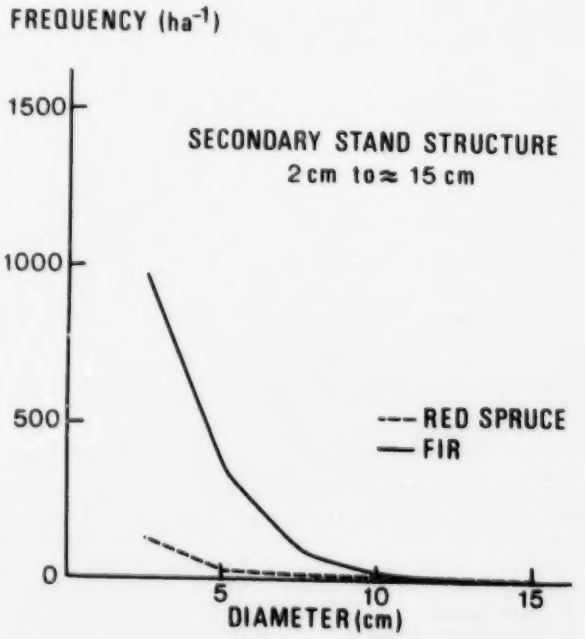

Figure 35. Secondary stand (rising understory) structure, red spruce-fir.

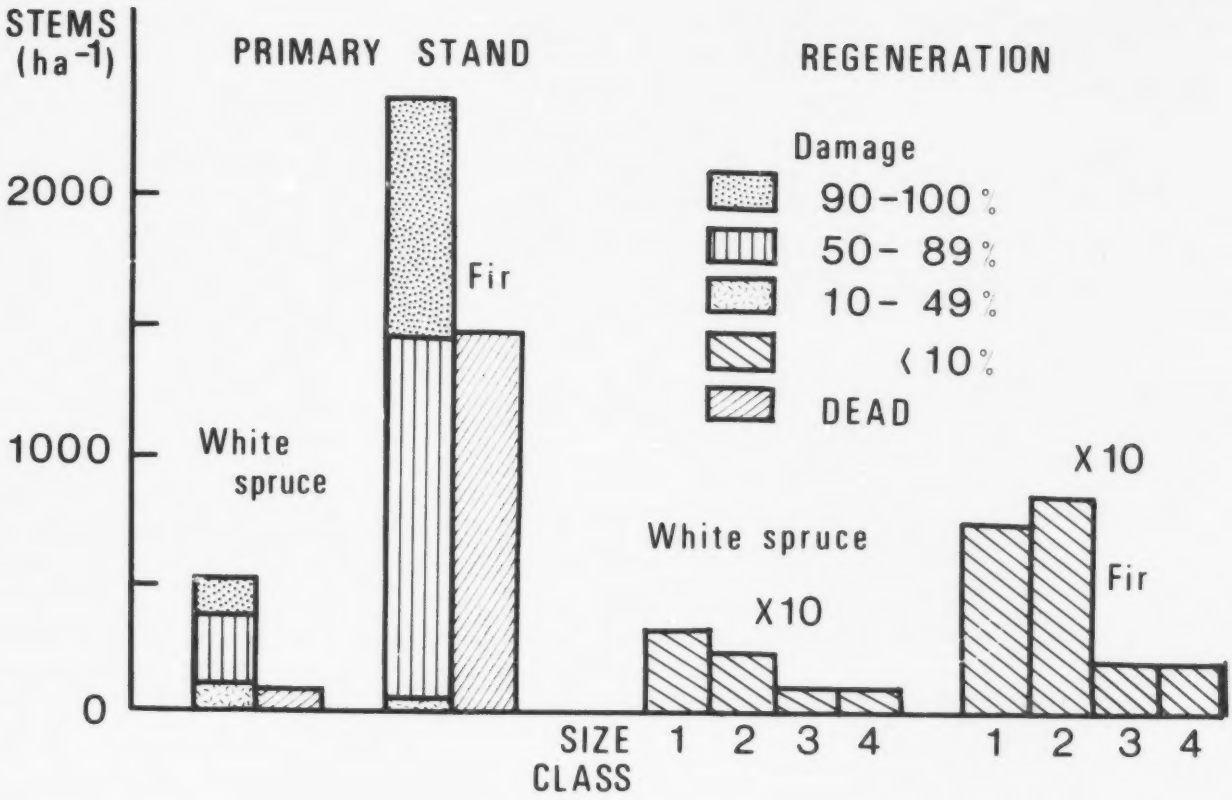

Figure 36. White spruce-fir stand structure (1979) following budworm attack. Primary stand includes standing dead, residual overstory, dead and damaged secondary understory.

centimetre classes, there are 1500 to 500 per hectare, respectively. This is a ratio of about 7:1 fir to spruce in the younger part of the stand. Such ratios commonly occur up to 10 or 12:1. The young fir are growing aggressively and, as expected, as this regeneration wave rises in the stand, the numbers of the small spruce will drop still further through competition from the fir.

Figure 33 illustrates the primary stand structure of the red spruce-fir forest. As in the preceding example, there are only small numbers of trees in the 45-65 centimetre diameter classes, and like the white spruce-fir stand, there are almost 20 trees per hectare in each of the centimetre classes between 10 and 20 in the red spruce-fir stand. Unlike the preceding stand, however, the red spruce-fir carry more individuals in the classes between 20 and 40 cm. This is compensated for by the slightly lower frequency in the 10-20 centimetre classes. Stands are roughly in the same state of development, however, and the fir has reached the 15 cm size class. The ratio of the fir to spruce in the rising regeneration wave in the 5-8 centimetre classes is about 8:1 fir to spruce. It is clear from this that as the small trees rise, the great preponderance of fir will be sustained and there will be some losses in the numbers of small spruce, again through competition with fir. In both of the cases illustrated, it is clear that the ensuing stands will be very much dominated by fir.

Figures 34 and 35 permit closer examination of the secondary stand between 2 and 15 centimetre diameter classes. Ratios of fir to spruce remain relatively constant by diameter class as indicated in the foregoing.

Figure 36 illustrates the relationship between the primary stand and the residual regeneration developing under it in white spruce-fir. The primary stand here contains the residuals destroyed and damaged by the budworm and also the rising secondary stand trees comprising the large numbers of fir and the much smaller numbers of spruce in the ratio of 7:1 in the very small diameter classes (2-15 cm). It is these trees which it is expected will form the next stand.

However, the structure of the regeneration which has formed underneath the primary stand is of interest. Regeneration has been divided into four size classes from 3 cm in height to 2 cm dbh. Here again, fir dominate, but it is imperative to scrutinize the relationship apparent in the 3rd and 4th regeneration classes from 45 cm in height to about 2 cm dbh. The ratio of fir to spruce is markedly different. In these critical size classes,

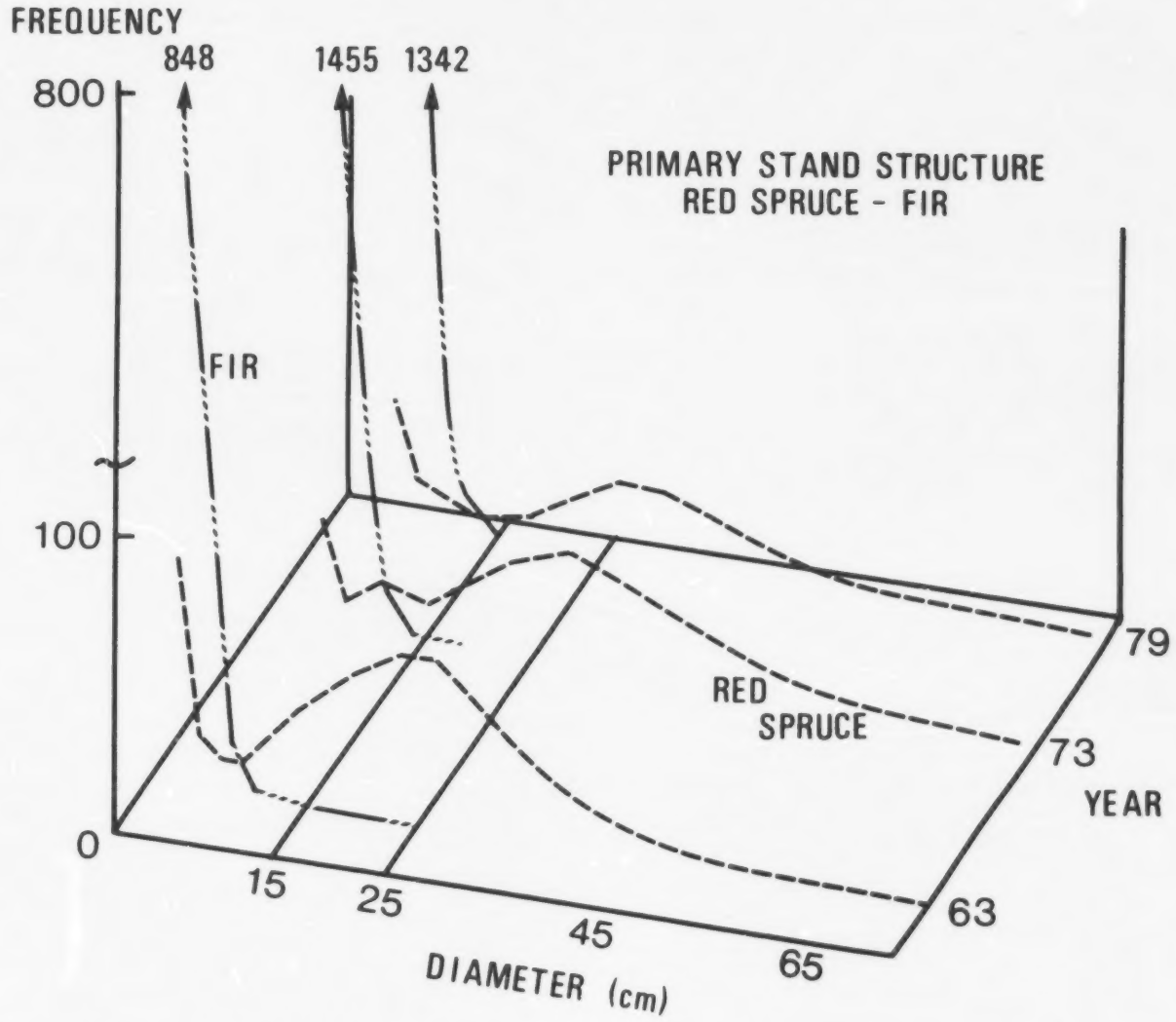

Figure 37. Red spruce-fir stand dynamics following the course of a budworm event.

the ratio is now 2:1 fir to spruce.

If the present overstory, including the rising secondary stand wave, were now wiped out, the stand would have a much more favourable composition of spruce relative to fir. The explanation for the shift in ratios in the regeneration is that despite the better seedling establishment characteristics of fir as compared to spruce, numbers of fir in the seed-bearing size in the original overstory have been totally eliminated by the massive preceding budworm event. This condition will prevail for many years, until such time as the rising wave of the secondary stand develops to a size which is consequent for flowering.

We have been privileged in being able to establish, monitor and work with data sets of long-term plots in spruce and fir. The great value of such long-term studies is clearly demonstrated as time goes on. These plots were initially established in 1959 and 1960 and are yielding very interesting data, some of which follows.

Figure 37 provides a model of the red spruce-fir forest showing stand dynamics through 16 years. It may be seen that for spruce the modal portion of the stand advances in this time period from 15-25 cm. There have also been some losses in numbers of individuals in spruce in the modal portion of the stand.

In the secondary portion of the stand, from 2-15 cm dbh, there were some initial losses in spruce, but their numbers have been holding and recently increasing slightly. Changes respecting fir are interesting. In the modal portion of the stand, fir reached 25 cm in 1963, but with ensuing remeasurements in 1973 and 1979, while the numbers had increased somewhat, fir became restricted to

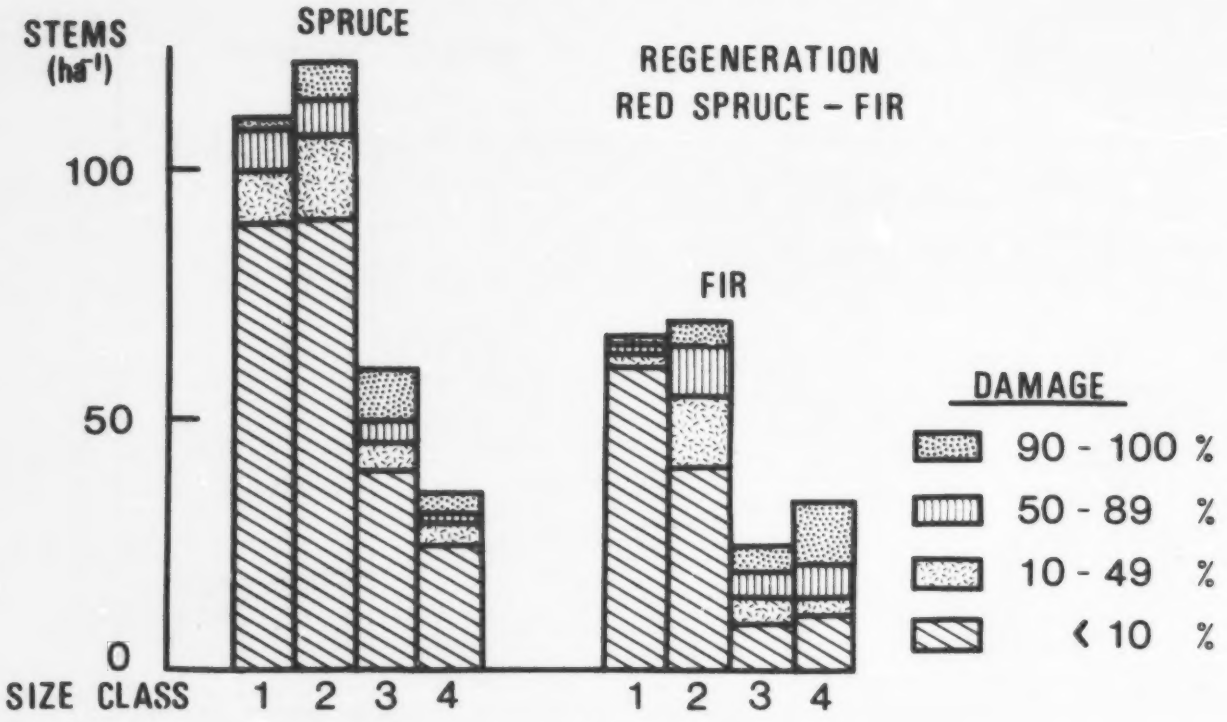

Figure 38. Red spruce and fir regeneration (1980) following a budworm event.

the classes below 15 cm, in fact, as we have seen from Figure 35, almost entirely to dbh size classes from 3-12 or 13 cm. The event which strongly influenced this stand development was a budworm buildup which initiated in 1971 and continued as a major outbreak through 1979.

Figure 38 presents data on the regeneration of the red spruce-fir forest. The regeneration is divided into size classes as above: the 3rd and 4th classes comprise seedlings from 45 cm to a metre in height, and one metre in height to 2 cm dbh. These are the most important in that they will be the size classes which, in most likelihood, will constitute the next stand. Damage categories are indicated, and what should be noticed are the differences in proportion of the budworm damaged to undamaged seedlings between spruce and fir. It may be seen that severely-damaged seedlings in the damage categories of 50% or greater, which will probably be eliminated as recruitment candidates for the future stand, constitute less than a quarter of both the 3rd and 4th size classes in the red spruce regeneration.

On the other hand, in the fir regeneration, more than a third in size class 3 and more than a half in size class 4 have been severely damaged and eliminated as recruitment candidates. The damage on the fir regeneration is twice as great as that on spruce in the last two size classes (3 and 4 combined) which, it will be recalled, are the trees now expected to enter the future stand. The higher numbers of spruce over fir in all regeneration classes is then an actual consequence of the budworm outbreak initiating in 1971.

It was noted in Figure 37 that fir was entirely eliminated between 1963 and 1979 from the 25 cm down to the 15 cm class, and most of it to lesser classes than that. Budworm not only reduced the fir in the stand largely down to size classes below flowering size, but also they would have interfered directly with flowering in those that were large enough to have flowers.

Since this data was collected, the process has continued to be played out. Current data coming in indicate that the secondary understory stand has indeed been heavily affected by budworm and large numbers of the fir have been totally eliminated. On the other hand, the spruce in that segment of the stand have to a large extent survived, and are still intact and growing. It will be seen that it is not, then, as was originally expected, the rising trees of the secondary understory stand (2-15 cm dbh) which will form or will even be desirable to form the next stand.

Figure 39 illustrates the red spruce stand overstory in 1959 with some old fir chicos still collapsing, and the rising secondary stand underneath consisting of almost pure balsam fir. The intensity of the outbreak in the secondary stand understory is shown in Figure 40 taken 20 years later in 1979. There are still surviving red spruce overstory trees, some of them damaged, some scarcely so, but balsam fir has almost entirely been eliminated.

Figure 39. Detail of red spruce-fir stand (1959). Overstory of red spruce, rising understory of pure balsam fir.

Figure 41 shows the interior of the red spruce-fir stand in 1979. The entire rising secondary or understory stand of small balsam fir is here seen to be totally stripped. There are hardly, if any, alive.

Figure 42 illustrates detail of a secondary understory stand in 1979, largely balsam fir, very heavily damaged or dead. A few still have some green foliage. A small red spruce about 1.5 metres high, and a single balsam fir about a metre are to

Figure 41. Interior of red spruce-fir stand. Rising secondary fir stand all stripped and dead.

be seen in the foreground in the rising regeneration class with very little damage and long well-developed leaders. The overstory red spruce are still fairly well intact. The red spruce in the secondary understory stand, about 5-8 metres in height, are alive and growing well.

In both the foregoing cases, the white spruce-fir and the red spruce-fir, a secondary budworm event has been substantially responsible for the maintenance of the spruce in the forest. Similar interpretations can be clearly deduced from the case history inventory data for the state of Maine

Figure 40. Red spruce-fir stand (1979). Red spruce overstory still surviving, balsam fir understory secondary stand all dead.

Figure 42. Detail of secondary understory red spruce-fir stand. Balsam fir all dead or dying; healthy red spruce regeneration dominating.

(Powell in press). I would propose that there are strong arguments for the co-evolution of the spruce budworm and the spruce-fir forest, and that where spruce and fir grow together, budworm are an essential factor in maintaining spruce in the stand through time.

Acknowledgements

I should like to acknowledge the unstinting support of my assistants, T. Norbert Lussier, Nancy Jondreau and Maria Famiglietti. I also wish to thank the many students of various disciplines who have assisted on our projects over the years, and my wife the late Jeanne Gordon who has supported and encouraged me in my work on spruce forests.

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Presents a technical update of the management of spruce-fir forests. Integrated management of eastern spruce budworm is not yet a reality. The ecological, social, and economic knowledge needed to develop an integrated management system is not available. The conference was designed to move individuals to a higher level of spruce budworm management in the eastern spruce-fir forests.